A proposed disease classification system for duck viral hepatitis

Xumin Ou,^{*,†,‡} Sai Mao,^{*,†,‡} Jingwen Dong,^{*,†,‡} Jiayi Chen,^{*,†,‡} Di Sun,^{*,†,‡} Mingshu Wang,^{*,†,‡} Dekang Zhu,^{*,‡,‡} Renyong Jia,^{*,†,‡} Shun Chen,^{*,†,‡} Mafeng Liu,^{*,†,‡} Qiao Yang,^{*,†,‡} Ying Wu,^{*,†,‡} Xinxin Zhao,^{*,†,‡} Shaqiu Zhang,^{*,†,‡} Juan Huang,^{*,†,‡} Qun Gao,^{*,†,‡} Yunya Liu,^{*,†,‡} Ling Zhang,^{*,†,‡} Zhijiang Miao,[§] Yunlong Li,[§] Yang Li,[§] Qiuwei Pan,^{§,#} and Anchun Cheng^{*,†,‡,1}

*Institute of Preventive Veterinary Medicine, Sichuan Agricultural University, Wenjiang, Chengdu, Sichuan, China; [†]Key Laboratory of Animal Disease and Human Health of Sichuan Province, Sichuan Agricultural University, Wenjiang, Chengdu, Sichuan, China; [‡]Research Center of Avian Disease, College of Veterinary Medicine, Sichuan Agricultural University, Wenjiang, Chengdu, Sichuan, China; [§]Department of Gastroenterology and Hepatology, Erasmus MC - University Medical Center Rotterdam, PO Box 2040, NL-3000 CA Rotterdam, the Netherlands; and [#]Biomedical Research Center, Northwest Minzu University, Lanzhou, China

ABSTRACT The nomenclature of duck viral hepatitis (**DVH**) was historically not a problem. However, 14 hepatotropic viruses among 10 different genera are associated with the same disease name, DVH. Therefore, the disease name increasingly lacks clarity and may no longer fit the scientific description of the disease. Because one disease should not be attributed to 10 genera of viruses, this almost certainly causes misunderstanding regarding the disease-virus relationship. Herein, we revisited the problem and proposed an update to DVH

disease classification. This classification is based on the nomenclature of human viral hepatitis and the key principle of Koch's postulates ("one microbe and one disease"). In total, 10 types of disease names have been proposed. These names were literately matched with hepatitis-related viruses. We envision that this intuitive nomenclature system will facilitate scientific communication and consistent interpretation in this field, especially in the Asian veterinary community, where these diseases are most commonly reported.

Key words: duck viral hepatitis, nomenclature

 $2022 \ Poultry \ Science \ 101:102042 \\ https://doi.org/10.1016/j.psj.2022.102042$

THE COMPLEXITY AND IRRATIONALITY OF THE DISEASE NAME OF DUCK VIRUS HEPATITIS

Since 1950, both classical and new duck hepatotropic viruses have been identified that cause a disease that was historically named duck hepatitis (**DH**) or duck viral hepatitis (**DVH**) (Stoute et al., 2020). Recently, we noticed 14 prototypes of viruses implicated in this disease, including 6 prototypes in the *Picornaviridae* family, 3 prototypes in the *Astroviridae* family, 2 prototypes in the *Flaviviridae* family, and 1 prototype each in the *Hepadnaviridae* family. In total, they belong to 10 genera among 6 viral families. It is generally not recommended to define a disease caused by more than one

Received December 29, 2021.

Accepted June 25, 2022.

genus of viruses. In this regard, this irrationality of the disease classification system challenges the key principle of Koch's postulates and Pasteur's conception. The disease-pathogen relationship is not followed by the principle of "one microbe and one disease" (Falkow, 1988). For example, although the viral names of duck hepatitis A virus (DHAV) and duck hepatitis B virus (DHBV) are different, they are both linked to the same disease name, DVH. There is no distinctive disease name specified by a defined hepatitis-related virus. This remains the main issue of the current disease naming compilation. To facilitate scientific communication and consistent interpretation, we revisited the historical definition of DVH and the corresponding causative viruses and proposed an intuitive classification system.

THE DISCOVERY AND HISTORICAL DEFINITION OF DUCK VIRAL HEPATITIS

In 1950, infectious viral hepatitis in ducklings was first described but not well defined by Levine and Fabricant

^{© 2022} The Authors. Published by Elsevier Inc. on behalf of Poultry Science Association Inc. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

¹Corresponding author: chenganchun@vip.163.com



Figure 1. Geographical distributions and host spectrum of DHAV and DHBV. (A) Geographical distribution of DHAV genotype 1 by country. (B) Geographical distribution of DHAV genotype 1 in China. (C) Host spectrum of DHAV genotype 1. (D) Geographical distribution of DHAV genotype 3 by country. (E) Geographical distribution of DHAV genotype 3 in China. (F) Host spectrum of DHAV genotype 3. (H) Geographical distribution of DHBV by country. (I) Geographical distribution of DHBV in China. (J) Host spectrum of DHBV. Appending sequence information from the NCBI virus database was used for geographical distribution and host spectrum analysis. In total, 226, 227, and 109 sequences matched DHAV genotype 1, DHAV genotype 3 and DHBV, respectively.

in Long Island, USA (Macpherson and Avery et al., 1957). In 1954, Asplin and McLauchlan also reported the same disease and first coined the term "duck virus hepatitis", as the gross lesions were limited to the liver (Asplin and Mclauchlan, 1954). Two years later (1956), the disease was transmitted to British Columbia, Canada (Macpherson and Avery et al., 1957). In 1971, this disease was further spread into Germany and Europe (Ulbrich, 1971), later into China (Wen et al., 2018), into Korea in 1985 (Kim et al., 2007), and recently into Egypt (Yehia et al., 2021). The disease was severe and caused sequential catastrophes in the duck industry. Then, researchers tried to isolate the causative virus by culturing it in duck embryos, chicken embryos, or corresponding primary cells (Pollard and Starr, 1960). After successful isolation of the duck hepatitis virus and subsequent observation by electron microscopy (Richter et al., 1964), the virus was designated duck hepatitis virus (DHV). This virus is identical to historically classical type I DHV and is now renamed duck hepatitis A virus (DHAV) (Kaeberle et al., 1961). However, certain early studies before 2019 also used duck hepatitis virus type 1 (or I) to describe DHAV or used those 2 names interchangeably (Kim et al., 2007; Liu and Kong, 2019).

The nomenclature DHAV was almost consistently used in later literature (Ou et al., 2017; Sui et al., 2022). DHAV was formerly classified as a member of the genus Enterovirus in the Picornaviridae family (Kim et al., 2006) and has historically been suggested to be a new genus that is genetically related to the genus Parechovirus (Ding and Zhang, 2007). It has now been classified into a new genus Avihepatovirus of the Picornaviridae family based on genetic evidence and International Committee on Taxonomy of Viruses (**ICTV**) classification (Zell et al., 2017). In addition, DHAV has been further divided into 3 different genotypes that are genetically and geographically different: the classically and globally distributed DHAV-1 and DHAV-2 in Taiwan and DHAV-3 in South Korea and China (Wen et al., 2014). This definition of DHAV genotypes was previously and is currently well recognized (Tseng et al., 2007; Liu et al., 2021). However, from 2012 to 2014, some literature used genotypes of DHAV-A, DHAV-B and, in particular, DHAV-C instead of genotypes DHAV-1, DHAV-2, and DHAV-3 (Zhang et al., 2012; Li et al., 2014). According to sequence appending information from the NCBI virus database, DHAV-1 and DHAV-3 were the main prevalent genotypes distributed

3

in Vietnam, Hungary, South Korea, and China, particularly Eastern China (Figures 1A–1F). The infected host species vary and are mainly limited to the Anatidae family (Figures 1C and 1F). With the isolated virus, a chicken embryo attenuated vaccine was developed by Asplin and provided 100% protection in ducklings (Asplin, 1965). However, a virus that was serologically and antigenically unrelated to "DHV" emerged in 1969, as vaccination of the chicken embryo attenuated vaccine did not provide complete immune protection (Toth, 1969). The emerging virus was subsequently proven to be duck astrovirus. In line with this observation, R E Gough 1985 reported an outbreak of type II DVHs, despite early descriptions by Mansi et al. in 1964 and Asplin in 1965 (Gough et al., 1985). During that time, Haider and Calnek (1979) also showed evidence of the occurrence of type III DVH, as the causative virus was antigenically unrelated to either type I or type II DHV. As reported, this virus has recently reemerged in China in 2021 (Wei et al., 2021). Type III DHV was previously suggested to be a member of the *Picornaviridae* family (Haider and Calnek, 1979). Of note, the causative virus of type II and III DVH is different from that of classical type I DVH. The genomic sequences of type II and III DHVs were different from those of type I DHVs with high evolutionary distance. Therefore, the original type II and III DHVs have been renamed duck astrovirus (**DAstV-1**) and duck astrovirus type-2 type-1 (DAstV-2), respectively, and they have both been classified into the Avastroviridae family (Fu et al., 2009). In 1980, DHBV was first discovered in Peking ducks, and its genome is DNA covered by a capsid and lipid envelope. However, early literature used the term "DHV" to describe DHBV, which caused misunderstanding regarding the causative virus itself because "DHV" remains an RNA virus and is not enveloped (Robinson, 1980). In addition, DHBV belongs to the genus Avihepadnavirus of the *Hepadnaviridae* family, while DHAV belongs to the genus Avihepatovirus of the Picornaviridae family (Zell et al., 2017). The misunderstanding was resolved 2 yr later, and since then, the term DHBV has been recognized and continually used in the hepatitis research community (Mason et al., 1983). Moreover, other names of DHBV-related viruses isolated from other host species in the Anatidae family have been also suggested, such as snow goose hepatitis B virus (literately named SGHBV) (Chang et al., 1999). The geographical distribution and host spectrum of DHBV are similar to those of DHAV (Figures 1H-1'J). Since then, 2 genera (Avihepatovirus and Avastrovirus) of RNA viruses (i.e., DHAV and DAstV) and one genus (Avihepadnavirus) of DNA viruses (i.e., DHBV) have been well recognized and linked to the same disease, DVH, which has made the virus-disease relationship in this regard unclear to some extent.

There are some neglected hepatitis-related viruses in ducks that cause only a minimal disease burden. These viruses were only tentatively named, as they generally did not cause a fatal outcome. The names of these viruses and their associated disease have not been clearly defined. Thus, the disease caused by these neglected viruses was described as being identical to "DVH". The disease name may inevitably be misused and may cause confusion to some extent in certain studies. For example, A Ponzetto in 1987 reported hepatitis delta virus (**HDV**) in Peking ducks that were coinfected with DHBV (Ponzetto et al., 1987). Coinfection between HDV and HBV commonly exists in humans, as HDV is a defective RNA virus that requires HBV to complete its life cycle (Miao et al., 2020). The nomenclature of duckderived HDV, as well as the corresponding disease name, was not well recognized or defined (Wille et al., 2018). In 1990, Chun-Hsien Tseng reported an outbreak of a DHAV-resembling virus that had a relatively large genome size (8,351 nt vs. 7,761 nt). This virus was originally suggested to be named "Avian sapelovirus" and was recently classified into the genus *Anativirus* of the *Picornaviridae* family (Tseng et al., 2007). Lili Chu in 2019 identified the first hepacivirus-like flavivirus in ducks and tentatively named it duck hepacivirus-like virus (DuHV) (Chu et al., 2019). Xiaoyan Wang in 2014 reported a virus closely related to DHAV but with low protein identity and, thus, suggested the tentative name 'Aalivirus', with 'Aalivirus A' as the type species (Wang et al., 2014). Qinfeng Liao in 2014 reported megrivirus-related viruses in ducks. Based on protein identities and genomic organization, duck-derived megriviruses, thus named duck megriviruses, and a new genus, *Megrivirus*, were suggested and were recently accepted by ICTV (Liao et al., 2014). Baoyuan Liu in 2018 reported infection of ducks by hepatitis E virus (**HEV**) by antibody evidence and RNA detection (Liu et al., 2018). In addition, human hepatitis G virus (also known as human pegivirus) is the causative agent of hepatitis G. It is possible that ducks can be infected by this type of pegivirus (tentatively DHGV), because we have recently identified this virus in geese, and geese and ducks belong to the same family Anatidae (Wu et al., 2020). Collectively, there are 14 prototypes of hepatitis-related viruses distributed in 10 genera of 6 families that are implicated in this disease, DVH (see Table 1).

A NEWLY PROPOSED CLASSIFICATION SYSTEM FOR DUCK VIRAL HEPATITIS AND ITS CAUSATIVE VIRUS(ES)

Human viral hepatitis diseases have been well defined by members of viruses in a defined genus, such as the disease-virus relationship between hepatitis A virus (**HAV**) and hepatitis A, as well as hepatitis B virus (**HBV**) and hepatitis B (Liao et al., 1991; Huang et al., 2016; Li et al., 2019; Miao et al., 2019). In total, 7 types of human viral hepatitis have now been indexed from hepatitis A to hepatitis G, named according to the alphabet of the hepatitis viruses (Table 1). Based on Koch's postulates and the conception of the human viral hepatitis classification system, we attempt to address

 Table 1. Classification of human viral hepatitis and proposed nomenclature for duck viral hepatitis.

Human			Duck				
Virus	Disease	Chinese disease name	Virus	Disease	Chinese disease name		
HAV HBV HCV HDV HEV HGV	Hepatitis A Hepatitis B Hepatitis C Hepatitis D Hepatitis E Hepatitis G	甲型肝炎 乙型肝炎 丙型肝炎 丁型肝炎 戌型肝炎 庚型肝炎	DHAV DHBV DHCV DHDV DHEV DHGV DuAa AAV-1 DAstV DuMV	Duck Hepatitis A Duck Hepatitis B Duck Hepatitis C Duck Hepatitis D Duck Hepatitis E Duck Hepatitis G Duck Hepatitis Aa Duck Hepatitis A_A Duck Hepatitis A_s Duck Hepatitis M	鸭甲型型肝炎 鸭内型型肝炎 鸭肉丁型肝炎 鸭皮型肝炎 鸭皮型肝炎 鸭季型型肝炎 鸭卵型肝炎 鸭卵型肝炎		

*The first letter of "卯" is "M" in its Chinese Pinyin code.

the naming complexity of DVH via a newly proposed classification system.

In our newly proposed system, 10 types of DVHrelated disease names that are caused by (possibly) 10 virus genera have been proposed. The redundancy of the causative viruses is attributed to multiple genotypes, such as genotypes of the genus Avihepatovirus and the genus Avastrovirus (Table 2). For example, we proposed that duck hepatitis A (DHA) was attributed to 3 genotypes of DHAV. Based on evolutionary analysis, 4 of 10 genera are closely related to members of the Picornaviridae family, while the remaining 6 genera in 5 different viral families have high evolutionary distance and less sequence coverage, except the genera Avihepacivirus and *Peqivirus* in the Flaviviridae family (Figure 2). To make a literal association between the disease names and all corresponding causative viruses (although some fit the standard), an intuitive disease-virus mapping system has been proposed, including DHAV and duck hepatitis A (**DHA**), DHBV and duck hepatitis B (**DHB**)

(Jilbert and Kotlarski, 2000), duck hepatitis C virus (**DHCV**) and duck hepatitis C (**DHC**) (Simmonds et al., 2005; Chu et al., 2019), duck hepatitis D virus (**DHDV**) and duck hepatitis D (**DHD**) (Miao et al., 2019), duck hepatitis E virus (DHEV) and duck hepatitis E (**DHE**) (Huang et al., 2016), duck hepatitis G virus (DHGV) and duck hepatitis G (DHG) (Wu et al., 2020), Aalivirus and duck hepatitis Aa (**DHAa**) (Wang et al., 2014), Avian anativirus 1 (AAV-1) and duck hepatitis A_A (**DHA**_A) (Tseng et al., 2007), DAstVs and duck hepatitis As (DHAs) (Fu et al., 2009; Chen et al., 2012; Liu et al., 2014), and duck megrivirus (**DuMV**) and duck hepatitis M (DHM) (Liao et al., 2014). Given that many Asian researchers focus on these diseases, the disease name in Chinese has accordingly been proposed by the order of the sexagenary cycle (ganzhi, "干支"), which is a traditional Chinese calendar used for reckoning time. This supplementary Chinese nomenclature system also obeys the same naming conception that is accepted by the Chinese hepatitis research community (Table 1).

Table 2. List of hepatitis-related viruses and proposed disease names.

Family	Genus	Species	Prototype	Tax ID.	Seq No.	Original disease name	Proposed disease name	中文病名
Picornaviridae	Avihepatovirus	Avihepatovirus A	DHAV-gt1	1006061	226	DH or DVH	DHA?	鸭甲型肝炎?
			DHAV gt2	1006062	2			
			DHAV gt3	1006063	227			
	Aalivirus	Aalivirus A	Aalivirus	2169685	3	DH or DVH	DHAa?	鸭辛型肝炎?
	Anativirus (Past Avian sapelovirus)	Anativirus A	AAV-1 (Past avian sapelovi- rus 1)	2759419	1	DH or DVH	DHA _A ?	鸭壬型肝炎?
	Megrivirus	Megrivirus A	DuMV	1330069	19	DH or DVH	DHM?	鸭卯型肝炎?
Hepadnaviridae	Avihepadnavirus	DHBV	DHBV	12639	109	DH or DVH	DHB?	鸭乙型肝炎?
Flaviviridae	Avihepacivirus?	Unclassified	duck hepacivirus (DHCV?)	2590836	4	Unclassified	DHC?	鸭丙型肝炎?
	Peqivirus	Unclassified	DHGV?	2830620	2	Unclassified	DHG?	鸭庚型肝炎?
Kolmioviridae	Avideltavirus?	Unclassified	DHDV?	2364132	1	Unclassified	DHD?	鸭丁型肝炎?
He peviridae	Orthohepevirus	Orthohepevirus B	DHEV?	2907992	2	Unclassified	DHE?	鸭戊型肝炎?
Astroviridae	Avastrovirus	Unclassified	DAstV-1	1239441	24	DH or DVH	DHAs?	
		Unclassified Unclassified	DAstV-2 DAstV-3?			DH or DVH DH or DVH		鸭癸型肝炎?

Tax ID., NCBI virus database.

Abbreviations: Aalivirus, Avihepatovirus/Avisivirus-like virus; AAV-1, Avian anativirus 1; DHAV-gt1, duck hepatitis A virus genotype 1; DHV-1, duck hepatitis virus type 1; DHA, duck hepatitis A; DH, duck hepatitis; DVH, duck viral hepatitis; DHA_a, duck hepatitis A; DHA_A, duck hepatitis A; DH, duck hepatitis; DVH, duck viral hepatitis; DHA_a, duck hepatitis A; DHA_A, duck hepatitis A_A; DuMV, duck megrivirus; DHM, duck hepatitis M; DAstV-1, duck astrovirus type 1; DHAs, duck hepatitis As; DHBV, duck hepatitis B virus; DHB, duck hepatitis B; DHCV, duck hepatitis C virus; DHC, duck hepatitis C; DHDV, duck hepatitis D virus; DHD, duck hepatitis D; DHEV, duck hepatitis E virus; DHE, duck hepatitis E; 中文病名, Chinese disease name;?, Proposed name.



Figure 2. Evolutionary relationships of 10 genera of hepatitis-related viruses in ducks. The evolutionary history was inferred using the neighborjoining method. Site coverage of these nucleotide sequences is displayed. The evolutionary distances were computed using the maximum composite likelihood method (below the branches). As the sequence of duck pegivirus is currently not available, goose pegivirus was used to construct the evolutionary tree. One thousand replicates of bootstrap tests were used for the statistics of the tree, and bootstrap values less than 70% were excluded. Six viral families are displayed in the right panel. The GenBank accession ID is displayed accordingly.

For emerging DVH-related viruses, we suggested assigning the name of the causative virus by the format of "duck hepatitis X virus, shortly DHXV", in which the X represents the first or the first 2 letter(s) of the causative viruses. When X overlaps or lacks identity, we suggest taking 2 letters to assign a distinct name for the disease and the causative virus, such as duck hepatitis A (DHA) and duck Aalivirus (DHAa) (Table 2). The corresponding disease name should be in the format of "duck hepatitis X, shortly DHX". However, in humans, the hepatitis F virus is a hypothetical virus and has not yet been substantiated (Deka et al., 1994). This deduction is attributed to the exclusion of any of the known hepatitis viruses. Thus, we suspended the disease name (i.e., duck hepatitis F, 鸭己型肝炎) in ducks that may be caused by possible "duck hepatitis F virus". The possibility of this disease awaits further verification by epidemiological and experimental evidence. In conclusion, we have proposed an intuitive disease classification system for explicitly indicating the disease and the causative virus, as well as the Chinese disease name. We hope this nomenclature system will facilitate scientific communication and consistent interpretation in this field, particularly in the Asian veterinary community.

ACKNOWLEDGMENTS

The Program Sichuan Veterinary Medicine and Drug Innovation Group of China Agricultural Research System (SCCXTD-2021-18), the earmarked fund for China Agriculture Research System (CARS-42-17), Science and Technology Program of Sichuan Province (2020YJ0396), and the National Natural Science Foundation of China (32102706) supported this work.

Availability of data and materials: The data that support the findings of this study are available in this manuscript.

DISCLOSURES

The authors declare no conflicts of interest that pertain to this study. REFERENCES

- Asplin, F. D. 1965. Duck hepatitis: vaccination against two serological types. Vet. Record 77:1529–1530.
- Asplin, F. D., and J. D. Mclauchlan. 1954. Duck virus hepatitis. Vet. Rec. 66:456–458.
- Chang, S.-F., H. J. Netter, M. Bruns, R. Schneider, K. Frölich, and H. Will. 1999. A new avian hepadnavirus infecting snow geese (Anser caerulescens) produces a significant fraction of virions containing single-stranded DNA. Virology 262:39–54.
- Chen, L., Q. Xu, R. Zhang, J. Li, Z. Xie, Y. Wang, Y. Zhu, and S. Jiang. 2012. Complete genome sequence of a duck astrovirus discovered in eastern China. J. Virol. 86:13833–13834.
- Chu, L., M. Jin, C. Feng, X. Wang, and D. Zhang. 2019. A highly divergent hepacivirus-like flavivirus in domestic ducks. J. Gen. Virol. 100:1234–1240.
- Deka, N., M. D. Sharma, and R. Mukerjee. 1994. Isolation of the novel agent from human stool samples that is associated with sporadic non-A, non-B hepatitis. J. Virol. 68:7810–7815.
- Ding, C., and D. Zhang. 2007. Molecular analysis of duck hepatitis virus type 1. Virology 361:9–17.
- Falkow, S. 1988. Molecular Koch's postulates applied to microbial pathogenicity. Rev. Infect. Dis. 10(Suppl. 2):S274–S276.
- Fu, Y., M. Pan, X. Wang, Y. Xu, X. Xie, N. J. Knowles, H. Yang, and D. Zhang. 2009. Complete sequence of a duck astrovirus associated with fatal hepatitis in ducklings. J. Gen. Virol. 90:1104–1108.
- Gough, R. E., E. D. Borland, I. F. Keymer, and J. C. Stuart. 1985. An outbreak of duck hepatitis type II in commercial ducks. Avian Pathol. 14:227–236.
- Haider, S. A., and B. W. Calnek. 1979. In vitro isolation, propagation, and characterization of duck hepatitis virus type III. Avian Dis. 23:715–729.
- Huang, F., Y. Li, W. Yu, S. Jing, J. Wang, F. Long, Z. He, C. Yang, Y. Bi, W. Cao, C. Liu, X. Hua, and Q. Pan. 2016. Excretion of infectious hepatitis E virus into milk in cows imposes high risks of zoonosis. J. Hepatol. 64:350–359.
- Jilbert, A. R., and I. Kotlarski. 2000. Immune responses to duck hepatitis B virus infection. Dev. Comp. Immunol. 24:285–302.
- Kaeberle, M. L., J. W. Drake, and L. E. Hanson. 1961. Cultivation of duck hepatitis virus in tissue culture. Proc. Soc. Exp. Biol. Med. Soc. Exp. Biol. Med. (New York, N.Y.) 106:755–757.
- Kim, M. C., Y. K. Kwon, S. J. Joh, S. J. Kim, C. Tolf, J. H. Kim, H. W. Sung, A. M. Lindberg, and J. H. Kwon. 2007. Recent Korean isolates of duck hepatitis virus reveal the presence of a new geno- and serotype when compared to duck hepatitis virus type 1 type strains. Arch. Virol. 152:2059–2072.
- Kim, M. C., Y. K. Kwon, S. J. Joh, A. M. Lindberg, J. H. Kwon, J. H. Kim, and S. J. Kim. 2006. Molecular analysis of duck hepatitis virus type 1 reveals a novel lineage close to the genus Parechovirus in the family Picornaviridae. J. Gen. Virol. 87:3307–3316.
- Li, C., Z. Chen, C. Meng, and G. Liu. 2014. Rapid detection of duck hepatitis A virus genotype C using reverse transcription loopmediated isothermal amplification. J. Virol. Methods 196:193–198.
- Li, Y., C. Qu, P. Yu, X. Ou, Q. Pan, and W. Wang. 2019. The interplay between host innate immunity and hepatitis E virus. Viruses 11:541–560.
- Liao, Q., L. Zheng, Y. Yuan, J. Shi, and D. Zhang. 2014. Genomic characterization of a novel picornavirus in Pekin ducks. Vet. Microbiol. 172:78–91.
- Liao, Y., Y. Lu, D. Lin, Y. Lee, S. Lee, and S. Chiu. 1991. The Outbreak and Control of Duck Viral Disease in Taiwan (1989-1990). Department of Epidemiology, Taiwan Provincial Research Institute for Animal Health, Tansui, ROC on Taiwan.
- Liu, B., M. Fan, B. Zhang, Y. Chen, Y. Sun, T. Du, Y. Nan, E. M. Zhou, and Q. Zhao. 2018. Avian hepatitis E virus infection of duck, goose, and rabbit in northwest China. Emerg. Microbes Infect. 7:76.
- Liu, N., F. Wang, and D. Zhang. 2014. Complete sequence of a novel duck astrovirus. Arch. Virol. 159:2823–2827.
- Liu, X., and X. Kong. 2019. Isolation, identification and attenuation of a pathogenic duck hepatitis virus type 1 in China, and complete genomic sequence comparison between the embryo-passaged, attenuated derivatives and their parent. Polish J. Vet. Sci. 22:163– 171.

- Liu, Z., Q. Ye, A. Cheng, X. Ou, S. Mao, D. Sun, S. Zhang, X. Zhao, Q. Yang, Y. Wu, J. Huang, Q. Gao, B. Tian, and M. Wang. 2021. A viroporin-like 2B protein of duck hepatitis A virus 1 that induces incomplete autophagy in DEF cells. Poult. Sci. 100:101331.
- Macpherson, L. W., and R. J. Avery. 1957. Duck virus hepatitis in Canada. Can. J. Comp. Med. Vet. Sci. 21:26–31.
- Mason, W. S., M. S. Halpern, J. M. England, G. Seal, J. Egan, L. Coates, C. Aldrich, and J. Summers. 1983. Experimental transmission of duck hepatitis B virus. Virology 131:375–384.
- Miao, Z., S. Zhang, Z. Ma, M. S. Hakim, W. Wang, M. P. Peppelenbosch, and Q. Pan. 2019. Recombinant identification, molecular classification and proposed reference genomes for hepatitis delta virus. J. Viral Hepat. 26:183–190.
- Miao, Z., S. Zhang, X. Ou, S. Li, Z. Ma, W. Wang, M. P. Peppelenbosch, J. Liu, and Q. Pan. 2020. Estimating the global prevalence, disease progression, and clinical outcome of hepatitis delta virus infection. J. Infect. Dis. 221:1677–1687.
- Ou, X., S. Mao, J. Cao, A. Cheng, M. Wang, D. Zhu, S. Chen, R. Jia, M. Liu, K. Sun, Q. Yang, Y. Wu, and X. Chen. 2017. Comparative analysis of virus-host interactions caused by a virulent and an attenuated duck hepatitis A virus genotype 1. PloS One 12:e0178993.
- Pollard, M., and T. J. Starr. 1960. Propagation of duck hepatitis virus in tissue cultures prepared with collagenase. J. Bacteriol. 80:571–572.
- Ponzetto, A., M. Rapicetta, B. Forzani, A. Smedile, C. Hele, G. Morace, A. M. di Rienzo, P. Palladino, L. Avanzini, and J. L. Gerin. 1987. Hepatitis delta virus infection in Pekin ducks chronically infected by the duck hepatitis B virus. Prog. Clin. Biol. Res. 234:47–49.
- Richter, W., E. Rdzok, and S. Moize. 1964. Electron microscopy of viruslike particles associated with duck viral hepatitis. J. Virol. 24:114–116.
- Robinson, W. S. 1980. Genetic variation among hepatitis b and related viruses*. Ann. N. Y. Acad. Sci. 354:371–378.
- Simmonds, P., J. Bukh, C. Combet, G. Deleage, N. Enomoto, S. Feinstone, P. Halfon, G. Inchauspe, C. Kuiken, G. Maertens, M. Mizokami, D. G. Murphy, H. Okamoto, J. M. Pawlotsky, F. Penin, E. Sablon, I. T. Shin, L. J. Stuyver, H. J. Thiel, S. Viazov, A. J. Weiner, and A. Widell. 2005. Consensus proposals for a unified system of nomenclature of hepatitis C virus genotypes. Hepatology 42:962–973.
- Sui, N., R. Zhang, Y. Jiang, H. Yu, G. Xu, J. Wang, Y. Zhu, Z. Xie, J. Hu, and S. Jiang. 2022. Long noncoding RNA expression rofiles elucidate the potential roles of lncRNA- XR_003496198 in duck hepatitis A virus type 1 infection. Front. Cell. Infect. Microbiol. 12:858537.
- Toth, T. E. 1969. Studies of an agent causing mortality among ducklings immune to duck virus hepatitis. Avian Dis. 13:834–846.
- Tseng, C. H., N. J. Knowles, and H. J. Tsai. 2007. Molecular analysis of duck hepatitis virus type 1 indicates that it should be assigned to a new genus. Virus Res. 123:190–203.
- Ulbrich, F. 1971. Transmission of duck virus hepatitis by wild ducks. Monatshefte Vet. 26:629–631.
- Wang, X. Y., N. Liu, F. M. Wang, K. Ning, Y. B. Li, and D. B. Zhang. 2014. Genetic characterization of a novel duck-origin picornavirus with six 2A proteins. J. Gen. Virol. 95:1289–1296.
- Wei, F., Y. Wang, Q. Wang, J. Yang, X. Jiang, D. He, Y. Diao, and Y. Tang. 2021. The isolation and characterization of Duck astrovirus type-1 remerging in China [e-pub ahead of print]. Transbound Emerg. Dis, doi:10.1111/tbed.14444. Accessed July 2022.
- Wen, H., L. Han, X. Zhang, C. Lian, L. Zhao, C. Si, and H. Chen. 2014. Duck hepatitis A virus (DHAV) genotype definition: comment on the article by Cha et al. Vet. Microbiol. 170:462–464.
- Wen, X., D. Zhu, A. Cheng, M. Wang, S. Chen, R. Jia, M. Liu, K. Sun, X. Zhao, Q. Yang, Y. Wu, and X. Chen. 2018. Molecular epidemiology of duck hepatitis a virus types 1 and 3 in China, 2010-2015. Transbound Emerg. Dis. 65:10–15.
- Wille, M., H. J. Netter, M. Littlejohn, L. Yuen, M. Shi, J. S. Eden, M. Klaassen, E. C. Holmes, and A. C. Hurt. 2018. A divergent hepatitis D-like agent in birds. Viruses 10:720.
- Wu, Z., Y. Wu, W. Zhang, A. Merits, P. Simmonds, M. Wang, R. Jia, D. Zhu, M. Liu, X. Zhao, Q. Yang, Y. Wu, S. Zhang, J. Huang, X. Ou, S. Mao, Y. Liu, L. Zhang, Y. Yu, B. Tian, L. Pan, M. U. Rehman, S. Chen, and A. Cheng. 2020. The first

nonmammalian pegivirus demonstrates efficient in vitro replication and high lymphotropism. J. Virol. 94:e01150-20.

- Yehia, N., A. M. Erfan, S. E. Omar, and M. A. Soliman. 2021. Dual circulation of duck hepatitis a virus genotypes 1 and 3 in Egypt. Avian Dis. 65:1–9.
- Zell, R., E. Delwart, A. E. Gorbalenya, T. Hovi, A. M. Q. King, N. J. Knowles, A. M. Lindberg, M. A. Pallansch, A. C. Palmenberg, G. Reuter, P. Simmonds, T. Skern, G. Stanway, and T. Yamashita. 2017. C. Ictv Report. 2017. ICTV

virus taxonomy profile: picornaviridae. J. Gen. Virol. 98:2421–2422.

- Zhang, H., J. Pi, C. Tang, H. Yue, and F. Yang. 2012. An experimental study of the pathogenicity of a duck hepatitis A virus genotype C isolate in specific pathogen free ducklings. Avian Pathol. J. W. V.P.A 41:613–620.
- Stoute, S. T, H.-J. Tsai, S. A. Metwally, A. Cheng, J.-L. Guérin, and V. J. Palya. 2020. Viral infections of waterfowl. Pages 446-497 in Diseases of Poultry. WILEY Blackwell, Hoboken, New Jersey.